

Responses of Ecosystem Carbon Cycling to Climate Change Treatments Along an Elevation Gradient

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ABSTRACT

Global temperature increases and precipitation changes are both expected to alter ecosystem carbon (C) cycling. We tested responses of ecosystem C cycling to simulated climate change using field manipulations of temperature and precipitation across a range of grass-dominated ecosystems along an elevation gradient in northern Arizona. In 2002, we transplanted intact plant–soil mesocosms to simulate warming and used passive interceptors and collectors to manipulate precipitation. We measured daytime ecosystem respiration (ER) and net ecosystem C exchange throughout the growing season in 2008 and 2009. Warming generally stimulated ER and photosynthesis, but had variable effects on daytime net C exchange. Increased precipitation stimulated ecosystem C cycling only in the driest ecosystem at the lowest elevation, whereas decreased precipitation showed no effects on ecosystem

C cycling across all ecosystems. No significant interaction between temperature and precipitation treatments was observed. Structural equation modeling revealed that in the wetter-than-average year of 2008, changes in ecosystem C cycling were more strongly affected by warming-induced reduction in soil moisture than by altered precipitation. In contrast, during the drier year of 2009, warming induced increase in soil temperature rather than changes in soil moisture determined ecosystem C cycling. Our findings suggest that warming exerted the strongest influence on ecosystem C cycling in both years, by modulating soil moisture in the wet year and soil temperature in the dry year.

Key words: warming; precipitation; gross ecosystem photosynthesis; ecosystem respiration; net ecosystem exchange; structural equation model.

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INTRODUCTION

Global mean temperature is predicted to increase 1.8–4.0°C by the end of this century, whereas estimates of projected precipitation are much more uncertain and region-specific (IPCC 2007). In the southwestern North America, multiple climate models predicted a drier climate throughout the current century as a result of rising greenhouse

gases (Seager and others 2007; Seager and Vecchi 2010). It is nearly certain that changes in temperature and precipitation will alter key ecosystem processes and ecosystem-level C exchange, and therefore will likely feed back to ongoing climate change (Cox and others 2000). To improve our predictive capability and allow human society to anticipate the magnitude of these impacts, we must: (1) assess the relative influence of these global changes, (2) determine whether global changes will produce antagonistic or synergistic interactions, and (3) determine the degree to which the answers to these questions is contingent upon the particular ecosystem being studied.

Temperature is a key driver of ecosystem processes, as demonstrated by a number of warming experiments. Warming has been shown to significantly increase soil respiration (Kirschbaum 1995; Lilley and others 2001; Mertens and others 2001; Emmett and others 2004; Niinistö and others 2004; Schindlbacher and others 2009), ecosystem respiration (ER) (Grogan and Chapin 2000), gross ecosystem production (Sullivan and others 2008), and net C uptake (Oberbauer and others 2007). Temperature can also negatively affect soil moisture content due to enhanced evapotranspiration, thus modulating the stimulating effects of increased temperature on ecosystem C cycling (McHale and others 1998; De Boeck and others 2007; Sherry and others 2008; Liu and others 2009). Meanwhile, precipitation is directly linked to ecosystem processes via soil moisture (Weltzin and others 2003). Enhanced precipitation has been shown to increase soil moisture (Risch and Frank 2007), photosynthesis (Liu and others 2009), and decomposition (Liu and others 2009), and can alleviate some negative effects of warming-induced soil drying. Soil moisture deficiency imposes stress on ecological processes such as photosynthesis (Deng and others 1990; Gorissen and others 2004) and respiration (Emmett and others 2004; Lellei-Kovács and others 2008). Field studies and models have demonstrated the importance of interannual precipitation variability in determining ecosystem-level productivity (Lieth 1973; Churkina and others 1999; Knapp and Smith 2001; Scurlock and others 2002; Huxman and others 2004; Garbulsky and others 2010). The majority of the above experiments have manipulated temperature or precipitation as single factors, yet few field studies have tested their interactive effects. Based on seven field manipulation experiments in forests, heathlands, and grassland, models suggest that two-way interactive effects of elevated temperature and doubled precipitation enhance ER and net primary

production (NPP), whereas NPP is depressed when elevated temperature is combined with reduced precipitation (Luo and others 2008). Although examples are few, most multi-factor field experiments have suggested that non-additive interactions between precipitation and temperature are negligible (Liu and others 2009; Dukes and others 2005; Zhou and others 2006; Grime and others 2008; Niu and others 2008a; Wu and others 2010).

To account for both rising temperature and altered precipitation effects on ecosystem C cycling, we conducted a plant–soil mesocosm (hereafter referred to as “mesocosm”) transplant experiment along the C. Hart Merriam elevation gradient in northern Arizona covering four ecosystems and a broad range of climatic regimes. This gradient has been used in numerous studies (Dijkstra and others 2006; Schwartz and others 2007; Adair and Schwartz 2008; Dijkstra and others 2008; Blankinship and others 2010) because its 7°C mean annual temperature range and 51-cm mean annual precipitation range lead to a wide variety of ecosystem types within a distance of only 50 km. We focused our studies on the grass-dominated vegetation across a 1064-m elevation range (1556–2620 m), including meadows in mixed conifer forests and ponderosa pine forests, grass-dominated interspaces in pinyon-juniper woodlands, and high desert grassland. A down-slope mesocosm transplant manipulation was initiated in 2002 to simulate projected warmer future temperatures. Because of the uncertainty of future precipitation change, two precipitation treatments (+50% and –30%) were applied to the mesocosms representing ranges of precipitation projections over North America (Christensen and others 2007). We measured components of ecosystem C cycling over two consecutive growing seasons of 2008 and 2009.

With this approach, we aimed to determine the relative importance of temperature and precipitation change on ecosystem C cycling and their interaction across multiple ecosystems. We hypothesized that: (1) elevated temperature stimulates gross ecosystem photosynthesis (GEP) and respiration in cooler ecosystems at high elevation, while suppressing these processes in warmer ecosystems at low elevation; (2) increased precipitation stimulates ecosystem C cycling more in drier ecosystems at low elevation than in wetter ecosystems at high elevation; and (3) warming combined with increased precipitation enhances net ecosystem C uptake, whereas warming with decreased precipitation reduces ecosystem C uptake.

METHODS

Mesocosm Transplant Experiment

Our study sites are located along the C. Hart Merriam elevation gradient in northern Arizona (Table 1; Online Appendix I—Figure A1; Blankinship and others 2010). Grass-dominated areas (10 m × 15 m) were selected in each of the four ecosystems and fenced to prevent grazing by cattle and elk. In 2002, we used a hardened steel corer to extract intact plant–soil mesocosms 30 cm diameter × 30 cm deep (all roots are above 30 cm) from the soil at each site. The 40 mesocosms from each ecosystem were placed intact into 30 cm diameter × 30 cm deep PVC cylinders, 20 mesocosms (treatment mesocosms) were then transplanted down-slope to the next lower (and thus warmer) site as the warming treatment, and the other 20 mesocosms (control mesocosms) were transplanted within the native site as control groups (Figure 1). Although disturbance effects may have occurred, comparisons of control and treatment mesocosms provided assessments of climate change treatment effects. Passive precipitation treatments at each site included a 50% increase, control, and a 30% reduction of annual precipitation ($n = 6$ or 7) spanning projections of precipitation changes over North America (Christensen and others 2007). For each mesocosm, precipitation was reduced using two clear acrylic channels, 5 cm wide that were fixed at a shallow angle 30 cm above the mesocosm to intercept and drain precipitation away from the mesocosm. The total area of the two channels was equal to 30% of the surface area of the mesocosm and therefore reduced the precipitation reaching the mesocosm by 30% during each rain event. Precipitation inputs were increased using a plastic rain collector mounted outside the mesocosm and connected by polyethylene tubing to redirect intercepted rain to the mesocosm. The collector area was 50% of the mesocosm area, supplementing

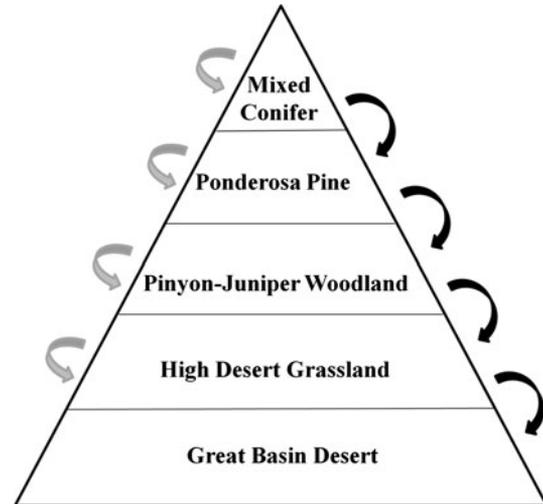


Figure 1. Mesocosm transplant experiment along the C. Hart Merriam elevation gradient to simulate elevated temperature. *Gray arrows* represent transplants within the same elevation as control groups, and *black arrows* represent the down-slope transplants to the next lower and warmer site along the elevation gradient. The Great Basin desert site is only used for its warmer temperature for high desert grassland mesocosms. Across all sites, downward transplant resulted in an increase in air temperature of 2°C.

precipitation by 50% during each rainfall event. To compensate for lower annual precipitation with the warming treatment, we also added a rain collector funnel for each transplanted mesocosm to simulate the precipitation level at the original site based on historical precipitation data. Because the precipitation difference between native and transplanted sites varied among ecosystems, the area of the rain collectors to compensate for lower precipitation at the transplanted site was site-specific. More site descriptions and experimental design information are available in Blankinship and others (2010) and Online Appendix I—Figure A1. A weather station (Campbell Scientific Inc., Logan, Utah) at each site

Table 1. Site Characteristics of Five Ecosystems Along the C. Hart Merriam Elevation Gradient

	Latitude	Longitude	Elevation (m)	Mean air temperature ¹ (°C)	Mean annual precipitation ¹ (mm)	Annual precipitation, 2008 (mm)	Annual precipitation, 2009 (mm)
Great Basin desert	35.69N	−111.43W	1556	13.2	154.5	154.8	145.8
High desert grassland	35.58N	−111.57W	1760	13.0	190.8	198.0	171.9
Pinyon-juniper woodland	35.50N	−111.62W	2020	10.5	282.1	317.9	228.0
Ponderosa pine forest	35.42N	−111.67W	2344	9.1	520.6	544.9	348.0
Mixed conifer forest	35.35N	−111.73W	2620	6.6	661.2	677.6	431.3

¹Based on weather station records at each site and gap-filled data from nearby weather stations for snow data from 2002 to 2010.

collected microclimatic variables including air temperature, precipitation, relative humidity, total shortwave radiation, and wind speed and direction.

Ecosystem C Flux Measurements

Ecosystem CO₂ fluxes were measured once per month from June to October in 2008 and in May 2009, and twice per month from June to August in 2009, using a static chamber method with a transparent 30 cm diameter × 30 cm height acrylic chamber that was sealed on top of the mesocosm cylinders and were interfaced to a LiCor 6400 (LI-COR, Lincoln, Nebraska) gas exchange system operating as a closed system. All sites exhibited a shorter growing season in the drier year of 2009, with peak biomass being reached in mid-August versus late-September in 2008. The CO₂ flux measurements were made between 9 am and 2 pm on cloud-free days at least 3 days after rain events in an attempt to capture intermediate and more common soil moisture conditions. At each measurement period, we first measured daytime net ecosystem exchange (NEE) of each mesocosm under ambient light, followed by ER (the sum of plant and soil respiration) in darkness. We calculated GEP as the sum of NEE and ER. The measurement of daytime NEE occurred over a period of 60 s during which CO₂ concentration was reduced by about 6 ppm. The chamber was then vented for 30 s, covered with a light-proof cloth, and ER was also measured over a period of 60 s, during which CO₂ concentration was increased by about 11 ppm. During each 60-s measurement period, fluxes were determined over six consecutive 10-s intervals with the average used for data analyses. A brief increase in leaf respiration, which is not representative of rates measured over longer periods of darkness, is sometimes observed immediately following a light-to-dark transition ([Atkin and others 2000](#)). We consider this potential artifact to be minor because our measurements also included stem, root, and soil microbial respiration, which are not known to exhibit a post-illumination burst. Moreover, CO₂ fluxes from ER were stable during the 60-s measurement period, indicating that any transient increase in leaf respiration following the light-to-dark transition had an undetectable contribution to the dynamics of total respiration. We were also aware of the possible errors associated with low CO₂ fluxes, yet we chose the 60-s measurement period to prevent chamber overheating. We used replication ($n = 6$ or 7) to separate signal from noise and installed a circulation fan inside the chamber to ensure thorough air mixing during the 60-s measurement period.

We conducted a time-weighted calculation to integrate monthly and bi-weekly fluxes into mean growing season fluxes. We calculated the products of average CO₂ flux rates and time span (in days) between the two adjacent sampling periods and then summed them over the entire growing season and divided by total number of days between the first and last sampling periods to get the time-weighted, growing season average CO₂ flux for each year. Because ecosystem gas exchange was measured in ambient light on cloud-free days, the integrated CO₂ fluxes likely represent maximum values for growing season NEE, ER, and GEP.

Climate and Environmental Conditions

There was less than 0.4°C difference in mean annual air temperature between 2008 and 2009 across all sites. However, precipitation differed strongly between the two years ([Table 1](#)). Annual precipitation in 2008 was higher than the 9-year (2002–2010) average across all sites, but much lower for 2009 ([Table 1](#)). In 2009, the actual precipitation deviated from the long-term average more at higher than lower elevation sites ([Table 1](#)). We also measured soil temperature, soil moisture, and photosynthetically active radiation (PAR) inside the mesocosms at the same time as (or immediately after) ecosystem C fluxes. Soil temperature at the center of each mesocosm at 15 cm depth was measured with a thermocouple, and light was measured by a PAR sensor on top of the chamber, both connected to the LiCor 6400 (LI-COR, Lincoln, Nebraska). We measured soil moisture by inserting a small theta probe soil moisture sensor at the center of the mesocosms at 6 cm depth (ML2x, Delta-T Devices Ltd., Burwell, Cambridge, England) immediately following the CO₂ flux measurements. The effect of disturbance from this insertion was minimal. The average environmental conditions during the gas exchange measurements are shown in [Table 2](#). We found less than 1°C change in temperature in the static chamber during the course of measurements for each mesocosm across all sites.

Statistical Analysis

To analyze interrelationships among our variables as a system, we used structural equation modeling ([Grace 2006](#)). Structural equation modeling is useful for partitioning relative strengths of direct and indirect effects of one variable on another and is widely used in ecological studies ([Weiher and others 2004](#); [Grace and others 2007](#); [Antoninka and others 2009](#); [Chaudhary and others 2009](#); [Laughlin and others 2010](#)). Our modeling approach

Table 2. Environmental Conditions During the Gas Exchange Measurements

	Photosynthetically active radiation ¹ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Air temperature ¹ (°C)	Relative humidity ¹ (%)	Soil temperature ^{1,*} (°C)	Soil moisture ^{2,*} (%)
Great Basin desert	1729 (86)	31.5 (1)	15.9 (4)	25.7 (0.2)	5.1 (0.2)
High desert grassland	1604 (86)	29.3 (2)	30.3 (8)	24.5 (0.1)	6.1 (0.3)
Pinyon-juniper woodland	1710 (27)	28.9 (2)	34.7 (9)	22.5 (0.3)	7.8 (0.3)
Ponderosa pine forest	1456 (123)	28.2 (2)	40.8 (8)	19.1 (0.1)	10.4 (0.8)
Mixed conifer forest	1485 (138)	24.1 (2)	41.2 (6)	15.5 (0.1)	12.0 (0.7)

Standard errors are in parentheses followed the means.

¹Recorded through LiCor 6400 during the gas exchange measurements and averaged over the growing seasons of 2008 and 2009.

²Based on soil moisture probe data from growing seasons of 2008 and 2009.

* $P < 0.001$ for one-way ANOVA of elevation effects on soil temperature and soil moisture.

is summarized only briefly here, but is more fully detailed in Online Appendix II. We developed an *a priori* conceptual model as a starting point for our modeling (Online Appendix II—Figure A2) and evaluated it using our data set, resulting in estimates of path coefficients and a test of validity of the model as an overall hypothesis. Path coefficients describe the strength of a hypothesized causal influence of one variable on another, and in their standardized form are directly analogous to partial correlation coefficients, or standardized regression weights. Because 2008 and 2009 were so different, we used a multi-group model with the two years as groups (Pugesek and others 2003; Grace 2006). This method allowed us to test differences between years in the relative strength and sign of pathways. A multi-group model starts with the hypothesis that the same model structure fits both groups and that the pathways are of equal sign and magnitude among groups (Grace 2006). The constraints are then relaxed one by one, allowing path coefficients or residual variances to take on different values in the different groups until the model fit is adequate. A χ^2 goodness-of-fit test is employed to test whether the model is a reasonable explanation of the patterns in the data; this test estimates the probability that the data fit the hypothesized model structure, thus a low probability value (commonly $P < 0.05$) indicates a poor fit. We confirmed adequate model fit with an additional test, the RMSEA (root mean squared error of approximation) index which adjusts for sample size and, thus, is broadly more informative. A value of the RMSEA of 0.05 or less would indicate a close fit of the model (Browne and Cudeck 1993), and the P value of the close fit is for testing the null hypothesis that the population RMSEA is no greater than 0.05, and therefore high P values indicate a close-fit model for the experimental data. All structural equation modeling was conducted in

AMOS 18.0 (SPSS Inc., Chicago, Illinois). We also used repeated measures ANOVA to statistically evaluate the effects of temperature, precipitation, time, and their interactions in Statistica 9.0 (Stat-Soft Inc., Tulsa, Oklahoma).

RESULTS

Environmental Variables

Soil temperature decreased and soil moisture increased with increasing elevation (Table 2). Soil moisture content was significantly affected by precipitation treatments ($P < 0.001$): mean soil moisture content was 9.4% in the control mesocosms, 11.4% in the increased precipitation treatment, and 7.4% in the decreased precipitation treatment. Combining the two years and all sites, down-slope mesocosm transplants (warming) significantly increased soil temperature relative to the source sites by 3.4°C ($P < 0.001$). Downward transplant increased soil temperature by different amounts in different ecosystems (Table 2), yet the magnitude of response to warming was not correlated with the soil temperature increase. Thus, we present responses to warming as simple treatment comparisons, warmed versus control.

Climate Change Treatment Effects on Ecosystem C Cycling

GEP, ER, and daytime NEE responded significantly to altered precipitation when all ecosystems and both years were combined (Table 3). We did not find a systematic variation of precipitation treatments effects along the elevation gradient (Table 3), contrary to our hypothesis that drier ecosystems at low elevation would show larger responses to precipitation. Combining both years and all ecosystems (interannual variability is discussed later), increased precipitation stimulated

Table 3. *F* ratios of Effects of Ecosystem, Temperature and Precipitation Manipulation, and Year on Gross Ecosystem Photosynthesis (GEP), Ecosystem Respiration (ER), and Daytime Net Ecosystem Exchange (NEE)

	Degrees of freedom	GEP	ER	NEE
Ecosystem	3	1.99	21.3***	6.69***
Temperature	1	9.42**	28.01***	0.03
Precipitation	2	12.73***	11.92***	6.57**
Ecosystem × Temperature	3	3.61*	2.79*	3.27*
Ecosystem × Precipitation	6	0.83	1.6	0.25
Temperature × Precipitation	2	0.87	0.48	1.57
Ecosystem × Temperature × Precipitation	6	1.39	0.91	1.18
Year	1	70.92***	35.76***	79.19***
Year × Ecosystem	3	49.19***	80.06***	10.79***
Year × Temperature	1	0.06	3.29	2.17
Year × Precipitation	2	2.3	0.88	3.9*
Year × Ecosystem × Temperature	3	14.84***	29.79***	2.25
Year × Ecosystem × Precipitation	6	0.52	1.37	0.43
Year × Temperature × Precipitation	2	0.39	0.52	0.14
Year × Ecosystem × Temperature × Precipitation	6	1.23	0.94	1.29

P* < 0.05, *P* < 0.01, ****P* < 0.001.

GEP on average by 18% ($0.26 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), ER by 17% ($0.15 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), and daytime NEE by 19% ($0.11 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), whereas decreased precipitation had no significant effects on ecosystem C cycling. In contrast to precipitation, the effect of temperature on ecosystem C cycling varied among ecosystems (Table 3). Warming significantly stimulated GEP and ER to the same degree in the high desert grassland and grassy interspaces in pinyon-juniper woodlands, with no significant change in daytime NEE when both years were combined (interannual variability is discussed later). In ponderosa pine forest meadows, warming significantly stimulated GEP more than ER, such that daytime NEE increased by $0.20 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. In contrast, meadows of mixed conifer forests responded to warming with significantly reduced GEP and increased ER, with daytime NEE decreasing by $0.15 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. No significant interactions between temperature and precipitation treatments were observed (Table 3).

Interannual Variability of Responses of Ecosystems C Cycling to Climate Change Treatments

Responses of ecosystems to climate change treatments differed in 2008 and 2009 (Table 3). The four ecosystems differed in responses to warming, and these responses differed between the two years (Table 3). For example, warming had contrasting effects on GEP and ER of grassy interspaces of pinyon-juniper woodlands between 2008 and 2009 (Figure 2). The effects of warming on GEP and ER

differed both in direction and in magnitude among ecosystems. In 2008, warming significantly increased both GEP and ER in high desert grassland and ponderosa pine forest meadows, reduced GEP and ER in grassy interspaces of pinyon-juniper woodland, and had no effect on meadows in mixed conifer forests. In 2009, warming increased GEP and ER in grassy interspaces of pinyon-juniper woodland and had no effects in the other three ecosystems (Figure 2). As a result, warming had no significant effect on daytime NEE in 2008, except for ponderosa pine forest meadows, and had no effects on daytime NEE in 2009, except in the high desert grassland (Figure 2). Overall, effects of warming on respiration and photosynthesis were similar in magnitude, with little effect on net C exchange.

Contrary to warming, effects of precipitation treatments were small and consistent between years (Figure 3). In 2008, only increased precipitation influenced ecosystem C cycling resulting in greater GEP and NEE in the high desert grassland and greater NEE in meadows in ponderosa pine forests (Figure 3A). Similarly in 2009, increased precipitation stimulated ER and GEP in the high desert grassland (Figure 3B), but precipitation treatments had no other significant effects on ecosystem C cycling.

Probing Mechanisms Using Structural Equation Modeling

General Mechanism of Responses of Ecosystem C Cycling to Climate Change Treatments

We developed a multi-group model for both years including all the mesocosms from four ecosystems

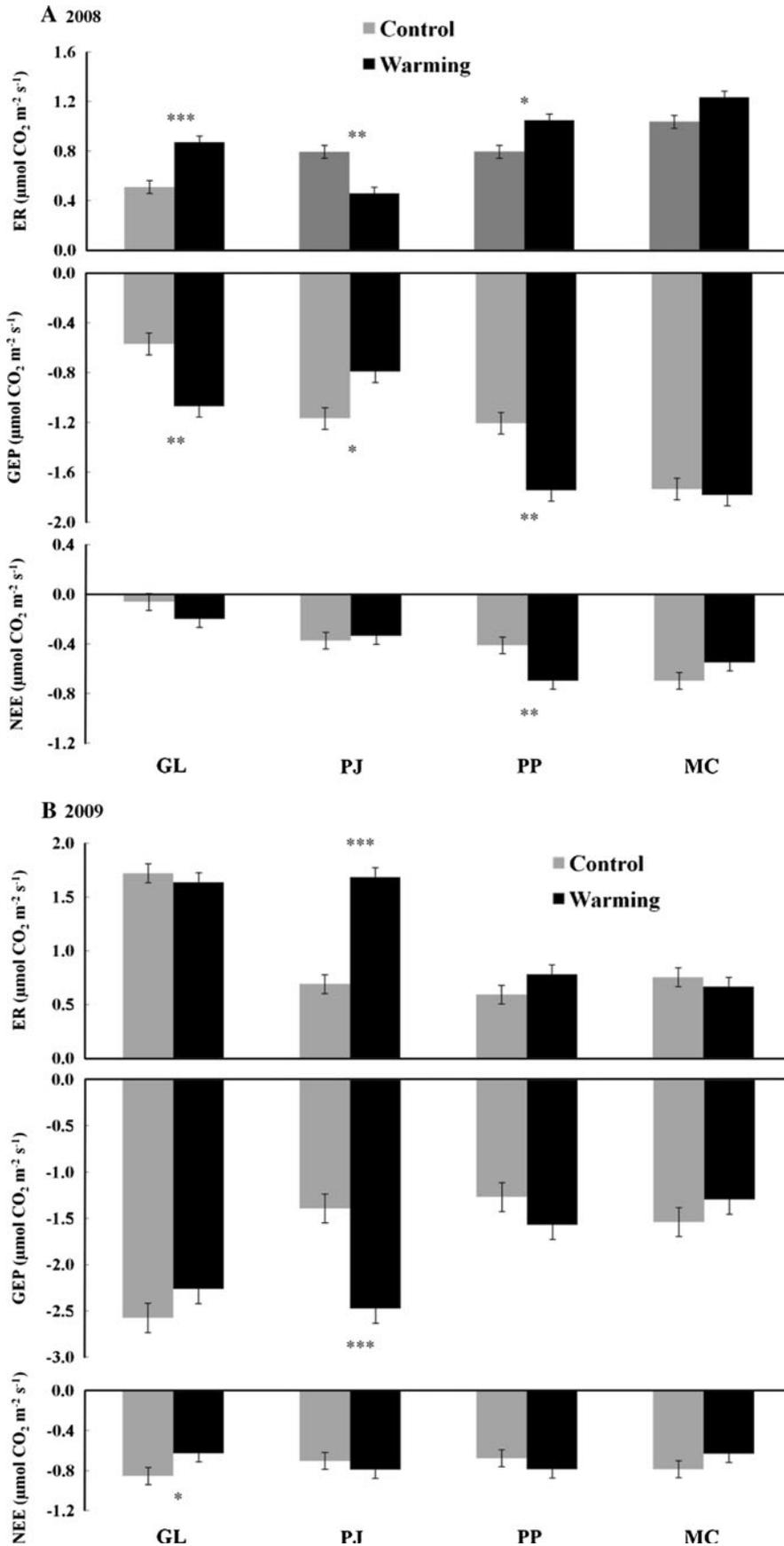


Figure 2. Warming (downward transplant) treatment effects on ecosystem respiration (ER), gross ecosystem photosynthesis (GEP), and daytime net ecosystem exchange (NEE) in growing seasons of **A** 2008 and **B** 2009. Positive numbers indicate carbon release from the ecosystems to the atmosphere, and negative numbers indicate carbon uptake from the atmosphere to the ecosystems. From lowest to highest elevation, four grass-dominated ecosystems are the high desert grassland (GL), grassy interspaces in pinyon-juniper woodlands (PJ), meadows in ponderosa pine forests (PP), and mixed conifer forests (MC). Error bars indicate standard error. Bars labeled * differ significantly from control groups (** $P < 0.001$, ** $P < 0.01$, and * $P < 0.05$).

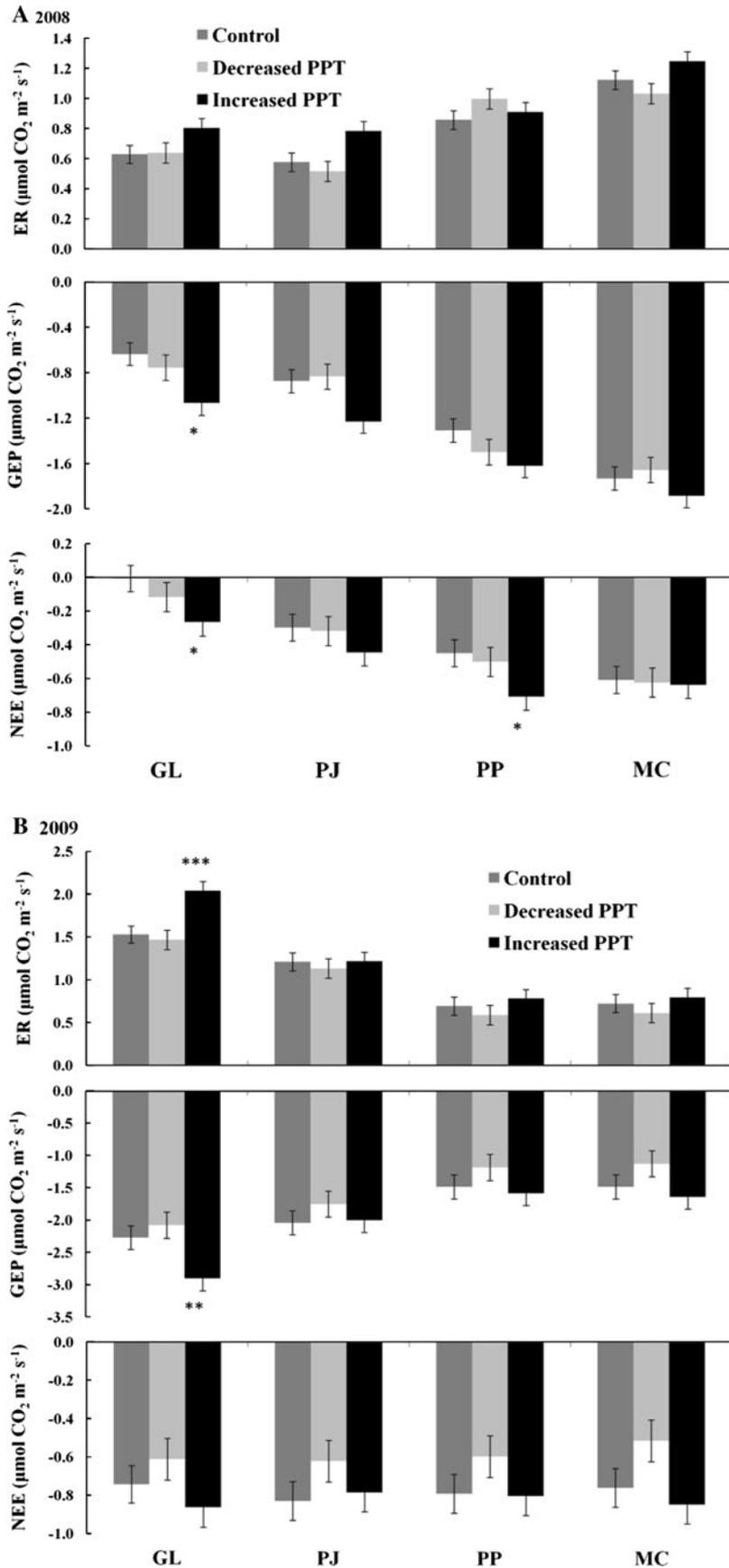


Figure 3. Precipitation (increased and decreased precipitations) treatments effects on ecosystem respiration (ER), gross ecosystem photosynthesis (GEP), and daytime net ecosystem exchange (NEE) in growing seasons of **A** 2008 and **B** 2009. *Positive numbers* indicate C release from the ecosystems to the atmosphere, and *negative numbers* indicate C uptake from the atmosphere to the ecosystems. From lowest to highest elevation, four grass-dominated ecosystems are the high desert grassland (GL), grassy interspaces in pinyon-juniper woodlands (PJ), meadows in ponderosa pine forests (PP), and mixed conifer forests (MC). *Error bars* indicate standard error. *Bars* labeled * differ significantly from control groups (** $P < 0.001$, ** $P < 0.01$, and * $P < 0.05$).

to probe the general mechanisms of ecosystem-level responses to climate change treatments (Figure 4). The model adequately fit the data ($\chi^2 = 37.9$, $P = 0.08$; RMSEA = 0.04, $P = 0.81$; $n = 160$).

First, 42% (2008) and 34% (2009) of the variation in ER was explained by this model (Figure 4). In 2008, soil moisture had a strong direct effect on ER (standardized path coefficient of 0.59; hereafter all standardized path coefficients are shown in parentheses); meanwhile, soil temperature had a strong indirect effect on ER (-0.54) through its effect on soil moisture (in addition to a small direct effect -0.09). Precipitation altered soil moisture (0.26), whereas warming altered soil moisture (0.43) and soil temperature (0.42). Thus, in 2008, soil moisture was the most important mechanism through which the climate change treatments altered ER. In contrast, soil temperature had a strong direct effects on ER in 2009 (0.61), followed by soil moisture (0.23). In 2009, precipitation greatly altered soil moisture (0.42) and warming increased soil temperature (0.42). Thus, in 2009, soil moisture was the variable controlling precipitation treatments effects on ER, and soil temperature was the more important factor determining warming effects on ER.

Second, 31% (2008) and 38% (2009) of the variation in daytime NEE was explained by the model (Figure 4). In 2008, soil temperature had a strong direct effect on daytime NEE (0.46), in addition to a minor indirect effect on daytime NEE (0.13) via soil moisture. Precipitation treatments altered soil moisture (0.26) and daytime NEE (-0.17), whereas warming altered soil moisture (0.43), soil temperature (0.42), and daytime NEE (-0.21). Thus, in 2008, soil temperature was the most important mechanism altering daytime NEE, and factors other than soil moisture were more likely to determine precipitation treatment effects on daytime NEE. Similar to 2008, soil temperature exerted the only strong direct effect on daytime NEE (0.47), and the indirect effect of soil temperature on daytime NEE was negligible (0.03) in 2009. Precipitation treatments altered soil moisture (0.42) and warming altered soil temperature (0.42), and the direct effects (other than affecting soil temperature and soil moisture) of climate change treatments on daytime NEE were negligible (-0.01 for precipitation and -0.03 for warming). Thus, soil moisture was the factor mediating precipitation treatment effects on daytime NEE, and soil temperature was the more important variable determining warming effects on daytime NEE.

Third, warming and precipitation treatments altered soil moisture differently in 2008 and 2009

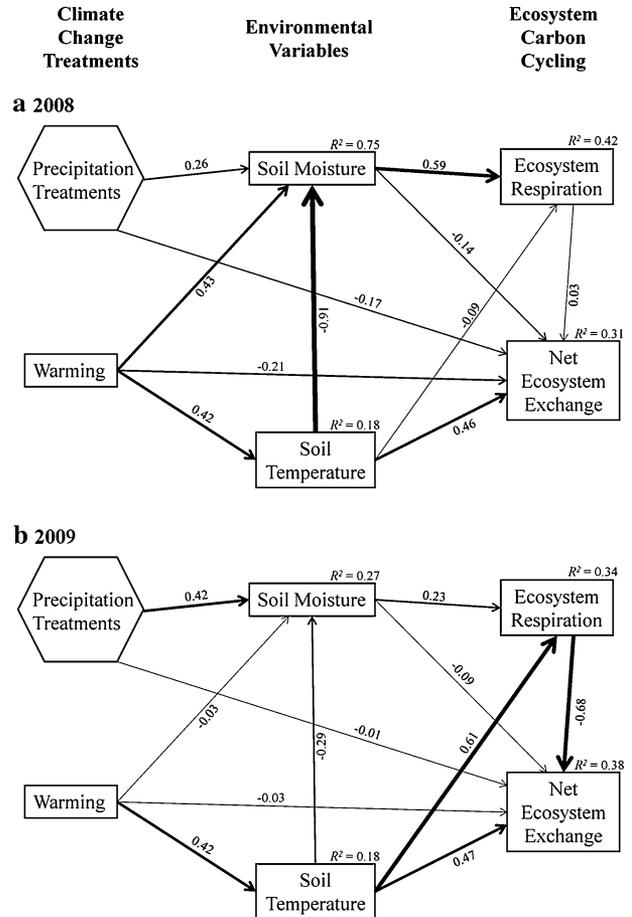


Figure 4. A structural equation model ($\chi^2 = 37.9$, $P = 0.08$; RMSEA = 0.04, $P = 0.81$; $n = 160$), showing how soil moisture and temperature influence components of C cycling in growing seasons of **A** 2008 and **B** 2009. Climate change treatments include altered precipitation (a composite variable which represents the additive effects of increased and decreased precipitation treatments) and warming (transplant). Environmental variables include soil moisture and soil temperature as simple measured variables. Ecosystem C cycling includes measured variables, ecosystem respiration, and daytime net ecosystem exchange. *Arrows* show the causal relationships and the *thickness of arrows* indicates the strength of the relationships. *Numbers* next to each arrow are the standardized path coefficients. R^2 values represent the proportion of variance explained by climate change treatments and/or environmental variables.

(Figure 4). In the wetter year of 2008, soil temperature had an overwhelming effect on soil moisture (-0.91) compared to the direct precipitation treatment effects (0.26). In contrast, in the drier year of 2009, precipitation treatments effects (0.42) rather than soil temperature (-0.29) had a larger effect on soil moisture.

Fourth, the contribution of GEP and ER to daytime NEE varied between the two years (Figure 4). In the wetter year of 2008, daytime NEE was primarily controlled by photosynthesis, indicated by the weak correlation between ER and NEE (-0.03). In contrast, in the drier year of 2009, ER largely determined daytime NEE (-0.68).

Fifth, warming affected ecosystem C cycling more than altered precipitation. In the wet year of 2008, warming had stronger direct and indirect effects on soil moisture than altered precipitation; warming had a strong direct effect on soil temperature, and both soil temperature and soil moisture affected ecosystem C cycling. In the dry year of 2009, warming had a strong effect on soil temperature, and soil temperature rather than soil moisture determined the ecosystem C cycling processes.

Responses of Individual Ecosystem to Climate Change Treatments

The structural equation modeling results showed that warming had the strongest effect on responses of ecosystem C cycling to simulated climate change through direct and indirect effects on soil moisture and temperature (Figure 4). Warming significantly increased soil temperature in all ecosystems during both growing seasons (Figure A3). However, warming had variable effects on soil moisture (Figure A4), due to the opposite direct and indirect effects of warming on soil moisture based on our structural equation model (Figure 4). In the wetter year of 2008, warming increased soil moisture in the high desert grassland (Figure A4a), leading to a positive effect on ER and GEP (Figure 2A). Warming reduced soil moisture in grassy interspaces in pinyon-juniper woodlands and decreased ER and GEP (Figure 2A). Warming had no effect on soil moisture in meadows in ponderosa pine forests (Figure A4a) and warming-induced increase in soil temperature led to the positive effects on ER and GEP (Figure 2A). Warming increased soil moisture in meadows in mixed conifer forests and tended to increase ER and GEP (Figure 2A). In the drier year of 2009, warming did not have a significant effect on soil moisture in the high desert grassland and meadows in ponderosa pine forests (Figure A4b) and warming had no significant effect on ER or GEP (Figure 2B). Warming had no significant effect on soil moisture in grassy interspaces in pinyon-juniper woodlands, but warming-induced increase in soil temperature led to an increase in ER and GEP (Figure 2B). Warming reduced soil moisture in meadows in mixed conifer forests (Figure A4b), compensated by positive effects of warming-induced

increase in soil temperature, resulting in no significant effect on ecosystem C cycling (Figure 2B).

In summary, in the wetter year of 2008, indirect effects of warming on soil moisture determined the responses of CO₂ fluxes in the high desert grassland and grassy interspaces in pinyon-juniper woodlands, especially the substantial reduction in soil moisture in pinyon-juniper woodlands; the direct effect of warming on soil temperature dominated the responses of CO₂ fluxes in meadows in ponderosa pine forests to warming. In the drier year of 2009, indirect effect of warming on soil moisture determined the responses of CO₂ fluxes in high desert grassland and meadows in ponderosa pine forests, whereas direct warming-induced increase in soil temperature dominated the responses of CO₂ fluxes in grassy interspaces in pinyon-juniper woodlands and meadows in mixed conifer forests to warming.

DISCUSSION

Warming Treatment Effects

Warming had variable effects on ER. Warming-induced increases in ER could stem from increases in C input from plant production (Luo and others 2009) and decomposition of soil organic matter (Hobbie 1996; Grogan and Chapin 2000; Melillo and others 2002; Neff and Hooper 2002), eventually leading to a net ecosystem C loss. However, such effects could be tempered by reduced leaf nutrient concentration and therefore lower litter quality (Jónsdóttir and others 2005), depletion of the soil labile C pool or reduced root and microbial activities due to warming-induced soil drying (Saleska and others 2003; Allison and Treseder 2008). Warming could also increase net nitrogen (N) mineralization and enhance vegetation growth, compensating for C losses from soils (Rustad and others 2001; Melillo and others 2002; Hartley and others 1999). We also observed that warming had variable impacts on GEP. In contrast to our results, warming reduced photosynthesis due to water stress in a grassland ecosystem in northern Belgium, whereas respiration remained unchanged, leading to a decline in net C uptake (De Boeck and others 2007).

Contrary to our hypothesis that cooler ecosystems at high elevation would show larger responses to warming than warmer ecosystems at low elevation, we did not find a systematic variation of response to warming treatments along the elevation gradient, indicating that the magnitude of ecosystem response to warming is not a simple

function of annual temperature. With the exception of the grassy interspaces in pinyon-juniper woodlands, warming had positive or no effects on GEP and ER. In the grassy interspaces in pinyon-juniper woodlands, warming had a negative effect on GEP and ER in 2008. The large warming-induced increase in soil temperature here (5.5°C) was likely responsible for the reduction in soil moisture from 11.1% in the control to 4.7% in the warmed mesocosms. According to our structural equation model, this moisture reduction underlies the negative effects of warming on GEP and ER in 2008.

A recent meta-analysis showed that across a broad range of terrestrial ecosystems, warming generally increased both GEP and ER, and had no effects on NEE (Wu and others 2010). There have been a number of studies using grassland model ecosystems to study these responses. Some showed grasslands as C sinks (Dugas and others 1999; Lawton and others 2006; Risch and Frank 2006; Soussana and others 2007; Mirzaei and others 2008; Chen and others 2009), C sources (Novick and others 2004; Bellamy and others 2005; Silver and others 2005; Schipper and others 2007), or near neutral (Frank and Dugas 2001; Suyker and others 2003), and such sink-source dynamics could be altered due to climate change (Scott and others 2010). Oberbauer and others (2007) showed that warming increased net C uptake in wet ecosystems, but increased C losses in dry ecosystems associated with higher ER. However, we only observed an increase in ER with warming in the dry ecosystem (high desert grassland) in the wet year (2008). Our results are similar to Bontti and others (2009), who found that increasing temperature only enhanced decomposition if precipitation is not limiting.

We did not observe a clear trend of responses of ecosystems to warming along the elevation gradient. However, we detected a critical role of soil temperature on daytime NEE. Given these disparate results, we may still be far from a generalized understanding of the responses of C exchange to increasing temperature for different ecosystems.

We also observed interannual variability of responses of ecosystems to warming. Based on our structural equation model results, soil temperature was found to be the most important factor controlling such differences between years. In the wetter year of 2008, soil temperature affected daytime NEE and indirectly affected ER via its influence on soil moisture. In the drier year of 2009, soil temperature directly affected ER and daytime NEE without altering soil moisture. Because the warming-induced increase in soil temperature has contrasting indirect (negative

through soil moisture) and direct effects (positive) on ecosystem C cycling, the relative strengths of the two effects determined responses of different ecosystems to warming between years. Based on the structural equation model, warming had an overall strong influence on ecosystem C cycling when all four ecosystems were pooled together, yet responses of ecosystem C cycling to warming varied among ecosystems and between years. In addition, the CO₂ fluxes were integrated over a longer period in 2008 because that year was wetter and had a longer growing season than 2009. Growing season duration is sensitive to climate change variables (Menzel and Fabian 1999), and our use of a time-weighted calculation for CO₂ fluxes was designed to account for this.

Furthermore, individual species are also very sensitive to interannual variability (Zavaleta and others 2003) and warming (Hobbie 1996), and species-specific responses were observed to changes in limiting resources (that is, moisture) as a direct effect of warming (De Valpine and Harte 2001), interacting with interannual temperature and precipitation variability to determine the direction and magnitudes of ecosystem-level responses. Microbial community and plant species composition shifts, and changes in soil labile C could also contribute to the responses of ecosystem C cycling to simulated climate change (Shaver and others 2000). Thus, it is important to conduct long-term ecosystem-level experiments to take into account composition shifts of species and possible feedbacks to ecosystem C cycling.

Precipitation Treatments Effects

The effects of increased precipitation on ecosystem C cycling are mostly non-significant except for the high desert grassland, indicating grassland ecosystems in the dry environment are most responsive to increased precipitation. We did not find any significant effects of decreased precipitation on ecosystem C cycling in both years, similar to the general responses across various ecosystems from a meta-analysis (Wu and others 2010). Contrary to our results, Mirzaei and others (2008) showed a reduction in CO₂ efflux due to drought in a grassland ecosystem, possibly because of lower enzyme activities from drought-induced soil moisture stress (Sardans and others 2008). We also observed stimulating effects of increased precipitation on ecosystem C uptake in the high desert grassland and meadows in ponderosa pine forests in 2008. In a semiarid steppe, increased precipitation stimulated photosynthesis more than respiration, leading

to net C gains (Liu and others 2009). A higher sensitivity of photosynthesis to soil moisture compared to that of respiration has been observed in other studies as well (Potts and others 2006; Chen and others 2009). In our systems, daytime NEE was predominantly determined by GEP in the wet year of 2008, whereas ER had a larger influence on daytime NEE in the dry year of 2009, indicating photosynthesis is more moisture-sensitive than respiration.

Based on the structural equation modeling of precipitation effects, soil moisture influenced responses of ecosystem C cycling to precipitation manipulation, similar to findings in a semiarid steppe (Chen and others 2008). Unlike the effects of warming-induced increase in soil temperature on ecosystem C cycling, precipitation directly altered soil moisture, and soil moisture directly affected ecosystem C cycling. Consistent with our hypothesis, the driest ecosystem at the lowest elevation was the most responsive to a simulated increase of precipitation, with ER and GEP increasing in both years, indicating that high desert grassland ecosystems in this region could be the most sensitive to future precipitation change. We observed little interannual variability of responses of ecosystems to precipitation treatments, mostly due to the overall non-significant effects of precipitation. In contrast, interannual variability of precipitation strongly affected C cycling in other grassland ecosystems (Chou and others 2008; Niu and others 2008b), and responses of ecosystems to precipitation treatments may therefore show large interannual variability.

The frequency and magnitude of extreme weather events, especially extreme precipitation events, is likely to increase with climate change (Easterling and others 2000; IPCC 2007). In addition to the total precipitation quantity manipulated in our experiment, precipitation timing, seasonality (winter snow vs. summer rainfall), length, and frequency have been shown to alter responses of ecosystem C cycling (Knapp and others 2008; Chen and others 2009; Chimner and others 2010). For example, a longer and later wet season led to significant C losses from annual grasslands (Chou and others 2008). Additionally, soil respiration decreased more because of altered rainfall timing than reduced rainfall quantity (Harper and others 2005). Photosynthesis and respiration may also have different sensitivities to precipitation changes. For instance, heterotrophic respiration is more sensitive to variability in wet season length than photosynthesis in a Mediterranean annual grassland in California (Xu and Baldocchi 2004). Thus, precipitation timing, seasonality, length, and frequency could disproportionately affect photosynthesis and

respiration, and the fate of net C exchange under future extreme precipitation events is uncertain.

CONCLUSIONS

After 8 years of temperature and precipitation manipulation in grassland model ecosystems along an elevation gradient, warming stimulated or had no effects on GEP and ER except for grassy interspaces in pinyon-juniper woodlands, with small and inconsistent effects on net C exchange. Increased precipitation had no effects on GEP and ER except for the high desert grassland, indicating that grassland ecosystems in the dry environment could be the most sensitive to future precipitation change. Decreased precipitation had no effects on ecosystem C cycling in all ecosystems during both growing seasons. We found no interactive effects between warming and altered precipitation, suggesting single-factor manipulation experiments are important in understanding responses of ecosystems to climate change. Our structural equation model results suggest that precipitation treatments affected ecosystem C cycling mostly via soil moisture, whereas warming affected the same processes via both soil temperature and soil moisture. In the wetter year of 2008, warming had a stronger effect on soil moisture than altered precipitation; whereas in the drier year of 2009, warming directly affected soil temperature, which determined the ecosystem C cycling processes. Our findings suggest that, overall, warming rather than altered precipitation had the strongest effect on ecosystem C cycling, by directly affecting soil temperature and indirectly influencing soil moisture.

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